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# Important population viability analysis parameters for giant pandas (*Aliuropoda melanoleuca*)

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**Abstract:** Population viability analysis (PVA) is a tool to evaluate the risk of extinction for endangered species and aid conservation decision-making. The quality of PVA output is dependent on parameters related to population dynamics and life-history; however, it has been difficult to collect this information for the giant panda (*Aliuropoda melanoleuca*), a rare and endangered mammal native to China, confined to some 30 fragmented habitat patches. Since giant pandas are long-lived, mature late, have lower reproductive rates, and show little sexual dimorphism, obtaining data to perform adequate PVA has been difficult. Here, we develop a parameter sensitivity index by modeling the dynamics of six giant panda populations in the Minshan Mountains, in order to determine the parameters most influential to giant panda populations. Our data shows that the giant panda populations are most sensitive to changes in four female parameters: initial breeding age, reproductive rate, mortality rate between age 0 and 1, and mortality rate of adults. The parameter sensitivity index strongly correlated with initial population size, as smaller populations were more sensitive to changes in these four variables. This model suggests that demographic parameters of females have more influence on the results of PVA, indicating that females may play a more important role in giant panda population dynamics than males. Consequently, reintroduction of female individuals to a small giant panda population should be a high priority for conservation efforts. Our findings form a technical basis for the coming program of giant panda reintroduction, and inform which parameters are crucial to successfully and feasibly monitoring wild giant panda populations.

**Keywords:** Giant panda; PVA; Population parameter; Parameter sensitivity index

Population viability analysis (PVA) is a method used in the evaluation, conservation and management of rare and endangered species, especially small meta-populations (Brook, 2000; Li & Li, 1994; Li, 2003; Marris et al, 2002). Due to PVA's effectiveness in evaluating the risk of extinction and future population development, it is the preferred and most economical decision-making conservation tool (Chapman et al, 2001; Brook et al, 2002). In China, PVA has consequently been applied to conservation policy-making for many endangered species, such as the crested ibis (Nipponia Nippon; Li et al, 1996), water deer (*Cervus unicolor*; Xu & Lu, 1996), Hainan Eld's deer (*Cervus eldi*; Song, 1996) and the finless porpoise (*Neophocaena phocaenoides*; Zhang & Wang, 1999).

As a flagship species, giant pandas (*Aliuropoda melanoleuca*) attract worldwide conservation attention. Since the 1970s, the Chinese government has been actively protecting the giant panda, establishing 64 nature reserves covering an area of 3 200 000 ha (Ifeng, 2010). The third national survey of giant pandas from the State Forestry Administration (SFA, 2006), estimates there are 1596 individuals living in the field across six major Chinese mountain ranges: the Qinling, Minshan, Qionglai, Liangshan, and Greater and Minor Xiangling Mountains.

PVA has been applied to giant panda populations previously by Wei & Hu (1994b), Guo & Hu (1999), Ren et al (2002), Wang et al (2002), Zhang et al (2002, 2003), Yang et al (2007), and Zhu et al (2008). However, the accuracy of PVA depends on the quality of the population parameters used and the data collected from the field

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(Shaffer, 1990; Dennis et al, 1991; Reed et al, 1998). Accordingly, determining robust and reliable parameter estimates is the foundation of PVA. For giant pandas, an appropriate PVA requires the inclusion of 23 population parameters (Yang et al, 2007). Given that giant pandas are long lived, mature late, and have a narrow diet and low reproductive capacity, and that males and females are difficult to distinguish in the wild because of a lack of sexual dimorphism, determining accurate parameters for use on giant panda populations is difficult. These reasons explain why only ten of the more than 1 600 papers published on giant pandas in the Chinese scientific journal database CQVIP include PVA. Likewise, each of these ten papers are based on two life tables from Wei & Hu (1989) who used data from 69 skulls and teeth collected in Minshan, Sichuan from 1978 to 1986, data from 30 radio-collared individuals collected from 1985 to 1997 in Qinling, Shaanxi (Pan et al, 2001), and data from captive animals collected between 1986 to 1999 (Huang et al, 2001). Variation exists between these two tables, mainly regarding the estimate of initial female breeding age, female reproductive rates, female mortality rates between age 0 and 1, and the mortality rate of adult females. This incongruence raises serious questions about the precision of any PVA study's output regarding giant pandas (Ellner et al, 2002; Li, 2003).

Although PVA requires a number of population parameters, their influence on the final results varies (Lacy, 2000). A parameter sensitivity index measures the sensitivity of population fates to changes in parameter estimates (Pulliam et al, 1992). This index then determines the most important factors likely to affect the viability of a population, and can be used to prioritize research and spending towards factors of immediate importance.

Here, we decided to focus our study of PVA parameters on giant panda populations in the Minshan Mountain, the largest area of giant panda population and habitat, with significant meaning for giant panda conservation across China (SFA, 2006). We performed PVA for six populations of giant pandas inhabiting the Minshan Mountains to see which parameters most impact PVA results and the likely fate of those populations over the next 100 years, and to derive suggestions for more practical conservation and monitoring of giant panda populations.

## MATERIALS AND METHODS

### Study area

The Minshan Mountains (E103º08′24″–105º35′22″, N31º04′18″–33º58′28″, see Figure 1) are a giant panda stronghold, characterized by high peaks and deep valleys. The highest peak is Xuebaoding, at 5588 m above sea level. The most recent third survey of giant pandas conducted from 2001 to 2003 indicated that the Minshan giant panda population was approximately 600 animals, comprising six subpopulations separated by logging, traffic, and human activity (Hu, 2001; Colby et al, 2001). According to Yang et al (2007; Figure 1) the six subpopulations are referred to as Baihe (10 animals),

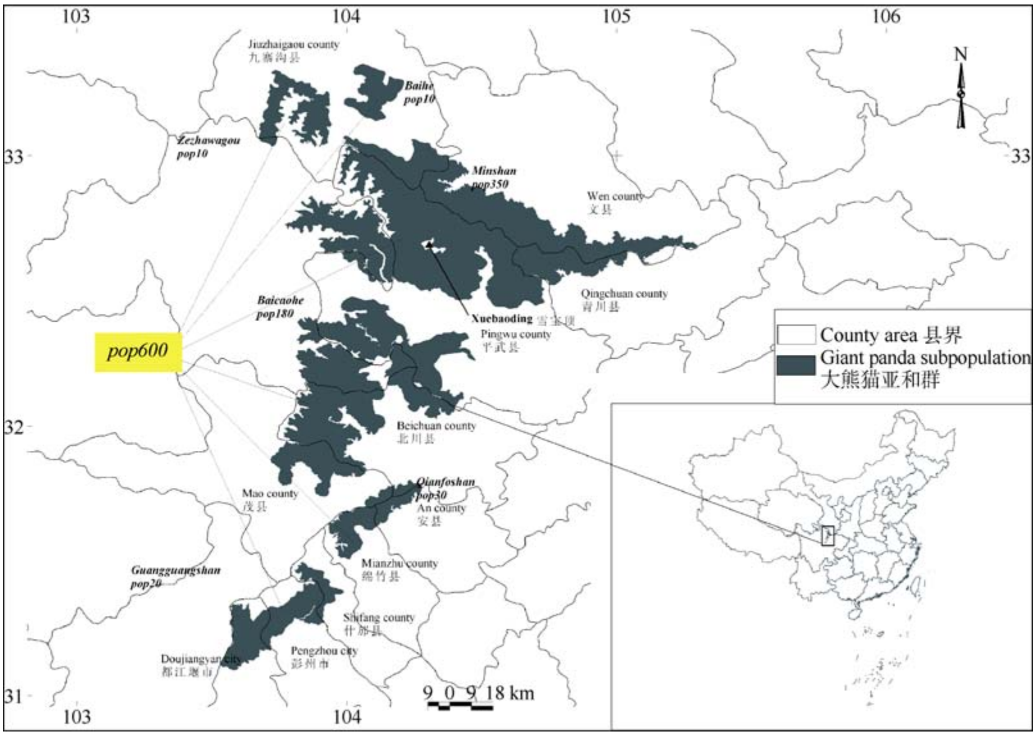


Figure 1 Estimates of giant panda population and six subpopulations in the Minshan mountains

Zezhawagou (10 animals), Minshan (350 animals), Baicaohe (180 animals), Qianfoshan (30 animals), and Guangguangshan (20 animals). We selected the Minshan Mountains for their important habitat to giant pandas, sustaining over 40% of the total wild population and representing 42% of total giant panda habitat (SFA, 2006; Yang et al, 2007). Likewise, the majority of population parameters were collected from this region (Wei et al, 1989; Wei & Hu, 1994a).

**Parameter sensitivity index**

We used VORTEX 9.41 to assess population viability of the six populations and produce statistical analysis on stochastic population growth rates, probabilities of extinction, average final population sizes, and genetic diversity. One thousand simulation runs for each set of parameters were conducted and persistence was projected over 100 years. We first used PVA for each of the six populations based on existing estimates of the required 23 parameters (Table1). We then performed sensitivity analysis for each population by changing one parameter and fixing the others. The parameter sensitivity ($S_x$) was calculated using the formula: $S_x = |(\Delta x/x)/(\Delta p/p)|$ (Li et al, 1997; Pulliam et al, 1992) where $x$ represents an initial size for a given population; $\Delta x$ represents the difference between initial size and the final size of the given population through PVA with changing parameters; $p$ is the initial value of a given parameter input into the PVA; $\Delta p$ is the value difference between $p$ and the value used in sensitive analysis, $\Delta x/x$ and $\Delta p/p$ represent the variation ratio of population size over 100 years with a given value of the parameter set.

**Table 1 Initial parameter values used in PVA**

| Extinction | First age of reproduction | Maximum breeding age (senescence) | Sex ratio at birth (percent males) | Polyandrous mating (%) | | Of those females producing progeny | | |
|---|---|---|---|---|---|---|---|---|
| No animals of one or both sexes | Females:7 Males:8 | 20 | 50 | % of adult males in the breeding pool = 100 | % of adult females in breeding pool = 62.5 | 93.33%of females produce 1 progeny in an average year | 6.67% of females produce 2 progeny in an average year | |
| Catastrophe type (Massive Death of bamboo) | | | | Initial populations size | harvest | supplementation | Inbreeding depression | |
| Frequency (as a percent): 1.67 | Multiplicative effect on reproduction = 91.4% (i.e.:1-8.6%) | | Multiplicative effect on survival = 91.4% (i.e.:1-8.6%) | 600, 350, 180, 30, 20, 10 | 10%, year 1 to year 100 at 10 year intervals | 10%, year 1 through year 100 at 10 year intervals | Omitted here | |
| Female mortality rates(%) and (Standard deviation) | | | | | | | | |
| Age1 | Age2 | Age3 | Age4 | Age5 | Age6 | Age7 | Age8 | Adults |
| 40.00 (10.0) | 9.67 (3.0) | 3.14 (2.0) | 1.52 (1.0) | 1.55 (1.0) | 1.57 (1.0) | 1.6 (1.0) | — | 13.33 (3.0) |
| Male mortality rates (%) and (Standard deviation) | | | | | | | | |
| Age1 | Age2 | Age3 | Age4 | Age5 | Age6 | Age7 | Age8 | Adults |
| 40.00 (10.0) | 9.67 (3.0) | 3.14 (2.0) | 1.52 (1.0) | 1.55 (1.0) | 1.57 (1.0) | 1.6 (1.0) | 3.45 (2.0) | 14.16 (3.0) |

For a given parameter, the higher value obtained for $S_x$, the higher its influence on PVA results. To test the difference and degree of influence of each parameter, a hierarchical clustered analysis with squared Euclidean distance was done in SPSS v14. We used the single linkage (nearest neighbor distance) agglomerative clustering method to arrange these parameters into groups.

**Data input to VORTEX**

The initial parameters (parameter 1–20; see Table1) were based on data collected from long term field studies of Wei & Hu (1994a) and Huang et al (2001), and ecological meaning from Sun (2001) and Wei et al (1989). Following Yang (2007), we assumed that the catastrophes only included the massive death of bamboo and set the parameters around harvest and supplementation, 10% respectively. We assumed no density-dependent effect for reproductive rates and inbreeding depression, as no study has detected this for wild giant pandas in the Minshan Mountains.

We used population estimates from the most recent national survey of giant pandas as the initial size (SFA, 2006; Yang et al, 2007). We simulated fates of the total population of pandas in the Minshan Mountains by pooling all subpopulations, giving an overall population of 600 animals and assuming connectivity. Here, we named the populations by the number of animals: pop10, pop20, pop30, pop 180, pop350, and pop600, with pop10 illustrating both the populations of Baihe and Zezhawagou, and pop600 illustrating the pooled all subpopulations of the area. Data input for PVA is given in Table 1 and changes made to each parameter are in Table 2.

# RESULTS

**PVA of giant panda populations using current parameter estimates**

We found that pop350 and pop600 will survive for 100 years with a zero probability of extinction. On average, pop350 would comprise 804 animals and pop600 1 464 animals at year 100 (Table 3) with both populations retaining 99% genetic diversity. Pop180 will

**Table 2 Changes in population parameters based on initial values for calculating parameter sensitivity with the same degree of adding and lessening**

| Number | Parameter | Initial value | To add | To lessen |
|---|---|---|---|---|
| 1 | Female initial breeding age | 7 | 8 | 6 |
| 2 | Male initial breeding age | 8 | 9 | 7 |
| 3 | Female reproductive rate (%) | 62.50 | 75 | 50 |
| 4 | Female mortality rate between age 0 and 1 (%) | 40 | 48 | 32 |
| 5 | Female mortality rate between age 1 and 2 (%) | 9.67 | 11.6 | 7.74 |
| 6 | Female mortality rate between age 2 and 3 (%) | 3.14 | 3.77 | 2.51 |
| 7 | Female mortality rate between age 3 and 4 (%) | 1.52 | 1.82 | 1.22 |
| 8 | Female mortality rate between age 4 and 5 (%) | 1.55 | 1.86 | 1.24 |
| 9 | Female mortality rate between age 5 and 6 (%) | 1.57 | 1.88 | 1.26 |
| 10 | Female mortality rate between age 6 and 7 (%) | 1.6 | 1.92 | 1.28 |
| 11 | Mortality rate of adult females (%) | 13.33 | 15.9 | 10.67 |
| 12 | Male mortality rate between age 0 and 1 (%) | 40 | 48 | 32 |
| 13 | Male mortality rate between age 1 and 2 (%) | 9.67 | 11.6 | 7.74 |
| 14 | Male mortality rate between age 2 and 3 (%) | 3.14 | 3.77 | 2.51 |
| 15 | Male mortality rate between age 3 and 4 (%) | 1.52 | 1.82 | 1.22 |
| 16 | Male mortality rate between age 4 and 5 (%) | 1.55 | 1.86 | 1.24 |
| 17 | Male mortality rate between age 5 and 6 (%) | 1.57 | 1.88 | 1.26 |
| 18 | Male mortality rate between age 6 and 7 (%) | 1.6 | 1.92 | 1.28 |
| 19 | Male mortality rate between age 7 and 8 (%) | 3.45 | 4.14 | 2.76 |
| 20 | Mortality rate of adult males (%) | 14.16 | 16.99 | 11.33 |
| 21 | Harvest (%) | 10 | 20 | 1 |
| 22 | Supplementation (%) | 10 | 20 | 1 |
| 23 | Catastrophes (%) | 8.60 | 17.20 | 4.30 |

persist over 100 years with a probability of extinction of 0.01%, undergoing a theoretical increase to 381 animals and loss of 0.03% genetic diversity. The probability of extinction of pop30, pop20 and pop10 was 1.4%, 15.3% and 84.5%, respectively. Pop30 is predicted to suffer a 0.09% loss in genetic diversity, while pop20 and pop10 a 0.15% and 0.39% loss respectively. The stochastic population growth rate was positive in pop600, pop350, pop180 and pop30 and negative in pop10 and pop 20 (Table 3). We found that in populations of less than 30 animals, stochastic population growth rates were negative and genetic diversity loss was greater than 10% after 100 years. In effect, the populations of Baihe, Zezhawagou and Guangguangshan are unlikely to survive the next century.

### Parameter sensitivity index results

Table 4 lists sensitivity indices for our set of parameters ($S_x$). The $S_x$ values of the four parameters (female initial breeding age, female reproductive rate, female mortality rate between age 0 and 1, and mortality rate of adult females) was higher than all other parameters. Further, for a given parameter, the value of $S_x$ in a small population was greater than in a large population. Accordingly, the smallest population had the greatest $S_x$ value and the largest population had the smallest $S_x$ values (Figure 2; Table 4).

The hierarchical cluster analysis based on $S_x$ of 23 parameters resulted in two distinct clusters (Figure 3). One cluster comprised the four key parameters with the highest $S_x$, the second cluster included all remaining parameters. Within the first cluster, parameter influence was highest with female initial breeding age followed by female reproductive rate, then female mortality rate between age 0 and 1 and adult female mortality rate.

**Table 3 Changes in six giant panda populations over 100 years based on PVA**

| Population | Stoc-r | SD(r) | PE | $N_{100}$ | SD($N_{100}$) | GeneDiv | SD(GD) |
|---|---|---|---|---|---|---|---|
| pop600 | 0.009 | 0.044 | 0.000 | 1 464.61 | 604.07 | 0.9952 | 0.0006 |
| pop350 | 0.008 | 0.047 | 0.000 | 804.89 | 318.65 | 0.9917 | 0.0013 |
| pop180 | 0.008 | 0.050 | 0.001 | 381.6 | 159.18 | 0.9838 | 0.0033 |
| pop30 | 0.004 | 0.086 | 0.014 | 50.84 | 33.2 | 0.9113 | 0.0403 |
| pop20 | −0.001 | 0.111 | 0.153 | 28.26 | 28.8 | 0.8461 | 0.0714 |
| pop10 | −0.014 | 0.138 | 0.845 | 2.52 | 7.71 | 0.6183 | 0.1755 |

Stoc-r, SD, PE, GeneDiv and $N_{100}$ are abbreviations of stochastic population growth rate, standard deviation, probability of extinction, genetic diversity, and final average population size, respectively.

pop600 denotes the entire population, pop350, pop180, pop30, pop20 , pop10 comprise all subpopulations in Minshan Mountains. Pop10 denotes both the populations of Population names correlate with population sizes, with the same name and meaning in later tables.

## DISCUSSION

### Importance of female giant pandas

Our results indicate that female giant pandas play a critical role in the growth of populations, as the parameters found to most influence population viability were based on aspects of female biology. The polyandrous mating system of giant pandas may explain this importance (Pan et al, 2001). For example, if female initial breeding age is lowered, female reproductive rates increase, female infant mortality rates decrease, and the mortality rates of adult females decreases. In combination, these factors increase the number of reproductive animals and the chances of population growth are accordingly enhanced.

Females have also been found to be important for giant panda metapopulations (Yang, 2007). Harris (2004) concluded that adult females yield approximately five times the conservation benefit of proportional increases in reproductive output. The same study found that populations were more sensitive to changes in female mortality than female reproductive output. Our analysis does not concur. Survival rates of females may determine the pace at which a population grows, but a higher female reproductive rate will result in a faster growth rate, at least for small populations. The smaller the

**Table 4 Parameter sensitivity index for six populations of different sizes**

| No. | Parameter name | pop600 | pop350 | pop180 | pop30 | pop20 | pop10 |
|---|---|---|---|---|---|---|---|
| 1 | Female initial breeding age | ***4.03*** | ***6.13*** | ***5.28*** | ***6.72*** | ***12.41*** | ***37.98*** |
| 2 | Male initial breeding age | 0.48 | 0.35 | 0.07 | 0.22 | 0.44 | 1.44 |
| 3 | Female reproductive rate | ***4.79*** | ***4.3*** | ***3.86*** | ***4.48*** | ***7.05*** | ***14.84*** |
| 4 | Female mortality between age 0 and 1 | ***3.77*** | ***3.45*** | ***3.04*** | ***3.31*** | ***4.67*** | ***7.77*** |
| 5 | Female mortality between age 1 and 2 | 0.73 | 0.78 | 0.66 | 0.62 | 0.62 | 0.77 |
| 6 | Female mortality between age 2 and 3 | 0.4 | 0.15 | 0.23 | 0.12 | 0.35 | 0.84 |
| 7 | Female mortality between age 3 and 4 | 0.15 | 0.08 | 0.18 | 0.08 | 0.15 | 0.06 |
| 8 | Female mortality between age 4 and 5 | 0.46 | 0.09 | 0.14 | 0.13 | 0.24 | 0.94 |
| 9 | Female mortality between age 5 and 6 | 0.36 | 0.15 | 0.1 | 0.07 | 0.14 | 1.26 |
| 10 | Female mortality between age 6 and 7 | 0.61 | 0.09 | 0.17 | 0.14 | 0.15 | 0.34 |
| 11 | Mortality of adult females | ***3.88*** | ***3.43*** | ***3.06*** | ***3.55*** | ***5.17*** | ***10.32*** |
| 12 | Male mortality between age 0 and 1 | 0.42 | 0.07 | 0.11 | 0.06 | 0.08 | 0.67 |
| 13 | Male mortality between age 1 and 2 | 0.28 | 0.06 | 0.06 | 0.1 | 0.2 | 0.9 |
| 14 | Male mortality between age 2 and 3 | 0.48 | 0.04 | 0.12 | 0.15 | 0.13 | 0.35 |
| 15 | Male mortality between age 3 and 4 | 0.31 | 0.06 | 0.13 | 0.1 | 0.19 | 0.39 |
| 16 | Male mortality between age 4 and 5 | 0.11 | 0.15 | 0.03 | 0.1 | 0.2 | 0.28 |
| 17 | Male mortality between age 5 and 6 | 0.18 | 0.03 | 0.06 | 0.15 | 0.12 | 0.77 |
| 18 | Male mortality between age 6 and 7 | 0.43 | 0.04 | 0.06 | 0.12 | 0.2 | 0.61 |
| 19 | Male mortality between age 7 and 8 | 0.31 | 0.07 | 0.08 | 0.1 | 0.17 | 0.41 |
| 20 | Mortality of adult males | 0.6 | 0.07 | 0.04 | 0.16 | 0.39 | 1.27 |
| 21 | Harvest | 0.56 | 0.52 | 0.49 | 0.45 | 0.62 | 0.49 |
| 22 | Supplementation | 0.57 | 0.58 | 0.54 | 0.71 | 1.02 | ***5.17*** |
| 23 | Catastrophes | 0.13 | 0.02 | 0.03 | 0.02 | 0.04 | 0.14 |

Bold and italic values show a high influence on the result of PVA.

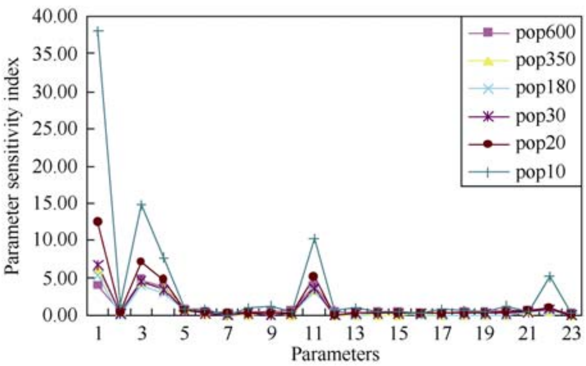


Figure 2 Parameter sensitivity index curve for six population sizes and four key female traits

Digits 1 to 23 in abscissa axis show 23 parameters respectively, as in Table 2.

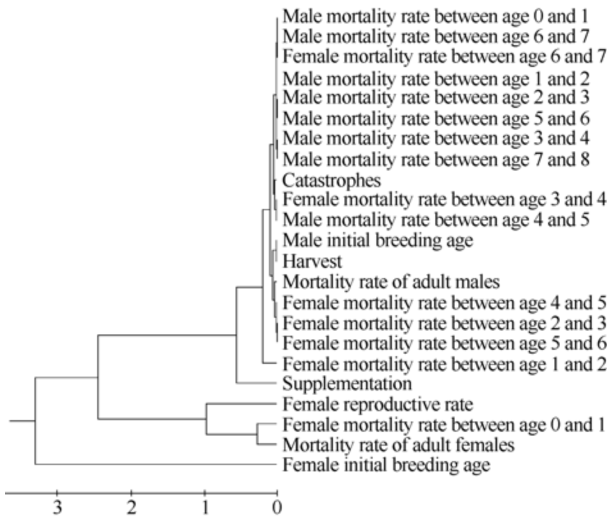


Figure 3 Hierarchical cluster analysis using the sensitive index of 23 parameters across six population sizes, indicating the two clusters based on the nearest neighbour distance of all parameters

population, the more critical female reproductive rate will be.

Previous PVA studies of giant pandas suggest that populations of less than 30 individuals are unlikely to survive 100 years (Wang et al, 2002; Yang et al, 2007). Our results concur, and indicate that the two subpopulations Minshan and Baicaohe can survive, but that the three subpopulations of Guangguangshan, Baihe and Zezhawagou will likely become extinct over the 100 years. Developing a conservation strategy for these small subpopulations is therefore urgently needed. Yang (2007) proposed supplementing small populations can greatly assist in their recovery, even at rates as low as one animal every 10 years. Most studies generally agree that any long-term population management strategy should aim for an annual extinction probability of less than 2% while maintaining more than 90% of current genetic diversity (Jiang, 1997). For small and vulnerable populations, such as those across the Minshan Mountains, the introduction of new animals may be necessary to avoid local extinction and maintain sustainable genetic diversity

The parameter sensitivity curves for the six population sizes show that each population experienced the same kind of change when the parameters were manipulated, but that parameters in small populations were relatively more influential. For example, the $S_x$ value of a given parameter for population pop10 or pop20 was double that for pop180 and three to six times greater than for pop350 (Figure 3). This factor was particularly evident for the key parameters that exert the most influence on PVA: female initial breeding age, female reproductive rate, female mortality rate between age 0 and 1, and mortality rate of adult females. When assessing the likely survival of giant panda populations through PVA, it is therefore crucial we ensure the validity of these four parameters.

## Management implications

Given the time and costs involved in collecting data to accurately determine life history parameters for models such as PVA, our results provide a basis for concentrating future conservation efforts and research on several key traits. We suggest current monitoring programs expand to include data collection on the four aspects of female biology we have identified here, as it is impossible to collect all population and life history data via current monitoring programs.

Our study also indicates that populations of less than 30 individuals may not survive the next 100 years. There are currently in excess of 260 captive giant pandas in China and some of these could be feasibly introduced to small wild populations. As our results illustrate, females provide a more significant contribution to population growth, a finding supported by simulations of dispersal of giant panda meta-populations in the Minshan Mountains (Yang et al, 2007). A bias towards male release may stem from the notion that male giant pandas are more robust and better suited for reintroduction; however, several failures of male release programs and the demographic importance of females shown here warrant a shift towards female release (Sohu, 2008). Additionally, an alternative strategy would be to enhance connectivity between subpopulations through habitat restoration and corridor construction. This would allow females to more easily disperse to new areas when leaving their natal environment (Pan & Lü, 1994).

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